

## The taxonomic status and zoogeography of *Cambarus bartonii carinirostris* Hay, 1914 (Crustacea: Decapoda: Cambaridae)

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*Abstract.*—Historically, *Cambarus bartonii carinirostris* was considered a subspecies of *Cambarus bartonii*. Recent studies indicate that *C. b. carinirostris* is indistinguishable from the nominate species and should be relegated to synonymy with *C. bartonii*. In other studies this assignment is not accepted and subspecific status has been maintained for *C. b. carinirostris* when reporting on crayfish closely related to *C. bartonii*. Work in the area of northern Appalachian crayfishes has made it apparent to us that *C. b. carinirostris* should be elevated to full species status based on its unique meristic and morphometric characteristics.

For nearly two decades we have studied the crayfishes of the northern Appalachians. Of the many questions associated with this area, the proper identity and distribution of *C. b. bartonii* (Fabricius 1798) has been and continues to be a principal concern. Ortmann's (1905, 1906, 1931) studies remain the foundation on which the distribution and systematics of northern Appalachian crayfish are presently understood. After Ortmann's death in 1933, Horton H. Hobbs, Jr., shifted the center of crayfish systematic studies to the southern Appalachians (and other southern areas) and the identity of *C. b. bartonii* and its subspecies remained unresolved. In the early 1970s we became interested in the ecology of crayfish in our home state, Ohio. We were immediately confronted with the problem of *C. b. bartonii* and the subspecies associated with it, since both *C. b. carinirostris* (Hay 1914) and *C. b. cavatus* (Hay 1902) are reported from Ohio (Hobbs 1974, 1989; Thoma & Jezerinac 1982). With the unresolved taxonomic problems and a domination by members of the subgenus *Cambarus* in Ohio, it became apparent that a taxonomic study

was needed before the study of crayfish ecology could commence.

### Materials and Methods

Specimens examined came from the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and the Ohio State University Museum of Biological Diversity, Columbus, Ohio (OSU-MBD). The paratypes, housed at the Museum of Comparative Zoology (MCZ) were not examined. Field collections (now housed at OSU-MBD) were made using a 1.3 × 2 m seine or by hand. A total of 95 specimens of *C. carinirostris* (33 Form I males, 27 Form II males, and 35 females) and 191 specimens of *C. b. bartonii* (79 Form I males, 43 Form II males, and 69 females) were measured for this study. Measurements were made to the nearest 0.1 mm using a vernier caliper and followed Hobbs (1981) and Jezerinac (1985). Measurements of regenerated body parts were avoided. Analysis was performed using SYSTAT 5.2.1. Principal component analysis used only Form I male specimens.

† Deceased, 21 April 1996.

*Cambarus* (*Cambarus*) *carinirostris* Hay,  
new status

*Cambarus bartonii carinirostris* Hay, 1914:  
384.

*Cambarus bartonii montanus*.—Faxon,  
1914:386 (in part).—Newcombe, 1929:  
286 (in part).

*Cambarus montanus montanus*.—Ortmann,  
1931:106 (in part).

*Cambarus* (*Cambarus*) *bartoni carinirostris*.—Ortmann, 1931:107.

*Cambarus* (*Cambarus*) *bartonii carinirostris*.—Hobbs 1969: 109, fig. 19m; 1974:  
11, fig. 24; 1989: 13 fig. 30.—Thoma,  
1982:875.—Thoma & Jezerinac, 1982:  
136.—Jezerinac, 1983: 4.—Jezerinac &  
Thoma, 1984: 120 figs. 8–9.—Jezerinac  
& Stocker, 1989: 2.—Jezerinac & Stocker,  
1990: 1.—Jezerinac, Stocker & Tarter,  
1995: 76–83, fig. 35–38.

*Diagnosis*.—Body pigmented. Carapace subcylindrical, slightly flattened dorsoventrally. Eyes slightly reduced. Rostrum with parallel or slightly concave margins, margins thickened, lacking marginal spines or tubercles, rostrum curved abruptly cephalically and terminating in upturned corneous tubercle; frequently with a median carina. Areola 3.4–12.0 times longer than wide (median = 5.7), comprising 25.2–40.4% of total length of carapace (median = 37.9%), bearing 3 to 4 punctations across narrowest part. Cervical spine absent or reduced to blunt tubercle. Cervical groove uninterrupted. Suborbital angle acute. Postorbital ridge lacking cephalic spine or tubercle. Branchiostegal spine reduced to small knob. Antennal scale approximately 1.5 times as long as broad, with mesial and lateral margins subparallel near and at midlength; distomesial margin strongly sloping. Basipodite of antenna lacking spine. Ischiopodite of antenna with blunt spine. Chela smooth, robust, length 79.6–111.9% of total carapace length (median = 94.0%) in Form I males (71.8–88.4%, median = 78.8% in females), bearing 1 row of 5 to 8 (median = 7.0) adpressed squamous tubercles along

mesial margin of palm and 5 to 7 punctations dorsal to such tubercles (occasionally distal 1 to 4 punctations replaced by tubercles). Width of gape of fingers of Form I male 17.4–46.3% of palm length (median = 27.2%), less so in Form II males (median = 16.3%) and females (median = 17.2%). Lateral margin of fixed finger weakly costate; moderately developed dorsomedial ridges on both fingers flanked by parallel rows of punctations; fixed finger impressed at dorsal and ventral lateral bases; dactyl 0.9–2.5 (median = 2.1) times longer than mesial margin of palm; palm width 41.5–51.1% (median = 46.1%) of chela length; third or fourth tubercle of mesial margin of fixed finger enlarged; 1–2 tubercles usually present on mid-subpalmar surface; never with elongated setae at base of fixed finger. Dorsomesial margin of carpus of chela with 1 distal spine and 1 proximal blunt tubercle; ventral surface with 1 or 2 conical tubercles at distal margin. Ventrolateral ridge of merus usually with 2–3 spines. Hook only on ischium of third pereopod of male. Basal boss on coxa of fourth pereopod well developed. First pleopods of Form I male contiguous at base, with 2 short terminal elements bent at approximately 90° to main shaft; corneous central projection truncated distally, bearing subapical notch; mesial process inflated, tapering distally; central projection of Form II male pleopods non-corneous, club-shaped. Females with annulus ventralis slightly embedded in sternum, asymmetrical, subrhomboid, slightly movable, lacking cephalolateral prominence; first through fifth pleopods similar in shape.

*Color notes*.—For the most part, this species is dorsally a uniform brown ranging from chestnut to tan with ventral surfaces fading to cream. Some populations have a greenish hue. The thickened rostral margins and postorbital ridges are a brownish red and the larger tubercles and spines orange. No banding or striping evident.

*Types*.—"Type" and paratypes USNM 23962 (1 Form I male, 7 Form II male, 15

female); paratypes, MCZ 7399 (1 Form I male, 1 Form II male, 1 female). The Form I male housed at the USNM is herein designated the lectotype of the species.

*Type locality.*—Hay (1914:385) stated “Gandy Creek, Oceola, Randolph Co., W. Va.” in his original description. A visit to this area and discussions with local residents indicated Oceola (38°42′50″N, 79°38′00″W) was the location of a now non-extant school house at the site of a historic lumber camp. The old school house was located near the Sinks of Gandy. We made a topotype collection from Gandy Creek upstream of County Road 40, just west of County Road 29/1 (38°43′22″N, 79°37′38″W). This site is the first road crossing downstream of the mouth of the Sinks of Gandy.

*Range.*—Found throughout the drainages of the Allegheny and Monongahela rivers in Pennsylvania, New York and West Virginia; tributaries of the Ohio River upstream of Sunfish Creek in Ohio and Fish Creek in West Virginia; southern tributaries of Lake Erie and Lake Ontario from the Grand River, Ohio, to the Genesee River, New York; throughout the Greenbrier River and tributaries of the New River upstream of the Greenbrier; upper Elk River, West Virginia.

*Variation.*—In the upper reaches of the Monongahela basin (Cheat and Tygart/Buckhannon basins) *C. carinirostris* probably retains its most plesiomorphic state. This is the only portion of the range in which no other stream dwelling forms of *Cambarus* are found. Here, *C. carinirostris* attains its greatest degree of sculpturing (including the carina) and approaches the body size of members of the subgenera *Cambarus* and *Puncticambarus* that inhabit larger rivers. The plesiomorphic appearance is likely in part due to the larger sizes attained. In the remainder of the range, *Cambarus* (*Puncticambarus*) *robustus* Girard, 1852, or *Cambarus* (*C.*) *sciotensis* Rhoades, 1944, occupy the larger mainstem streams and *C. carinirostris* is confined to the

smaller tributaries. In the Casselman River of the Youghiogheny River, Pennsylvania, we have seen specimens with body forms reminiscent of the subgenus *Erebicambarus* Hobbs, 1969, in that they display a more tubular, sausage-shaped carapace that is less dorsoventrally compressed. The chelae remain decidedly within the range of *C. carinirostris*, though they have the least amount of gape between the fingers. Specimens from the southernmost extent of the range display reduced inflation of the rostral margins and lack the 90° angle at the rostral tip. The rostra in this population most closely resemble the probable plesiomorphic state.

Occasionally, a second row of slightly produced tubercles can be found on the palm of the chela. This character does not exhibit a defined geographical pattern but appears in some individuals in most collections. All other populations exhibit the normal characteristics given in the Diagnosis.

*Size.*—Mature specimens range from 26 to 48.8 mm (median = 34.9 mm) total carapace length (median: Form I males 36.9 mm, Form II males = 31.9 mm, females = 35.4 mm).

*Life history notes.*—Jezerinac et al. (1995) reported Form I males from late April through early September and ovigerous females from July through mid August. This study found Form I males as late as October and ovigerous females in the reported range of dates. No information exists on longevity, growth rates, thermal preferences or dietary habits.

*Habitat and ecology.*—The normal habitat occupied by *C. carinirostris* is pools and riffles of high gradient first and second order streams. Populations can be found in intermittent streams but the abundance is greatly reduced. Some burrowing occurs, mostly sub-boulder, in mid-stream or on the edges of streams. This species is a secondary burrower. *Cambarus carinirostris* is capable of expanding its niche in the absence of other species of *Cambarus* that are primary burrowers or mainstem inhabitants.

Often caves, if present, yield specimens, usually in the vicinity of the mouth. This species is sensitive to excess silt, bed load sediments, nutrient enrichment, acid mine impacts, and habitat alterations that reduce cobble and boulder abundance.

*Taxonomic status.*—Numerous authors have commented on the distribution and taxonomic status of *C. carinirostris*. In his original description Hay (1914: 385) reported the species from Tygart Valley and Cheat River in Randolph County, West Virginia, stating that *C. carinirostris* was “. . . a well marked subspecies . . .” differing from the nominate species in that “. . . the carapace is a little more cylindrical, the rostrum broader and flatter, and always furnished near the tip with a median longitudinal carina.” Faxon (1914: 385), commented that the rostral carina was a rather elusive character and reported additional records for this taxon from the Greenbrier River basin (West Virginia). The next report on *C. carinirostris* was Ortmann (1931: 139) in which he retained the subspecific status for *C. carinirostris*, and stated *C. carinirostris* differs from *C. b. bartonii* only in the presence of the carina. After Ortmann’s death, no further comments were published on the taxonomy of *C. carinirostris* until Hobbs (1972: 111) commented that it probably should not be recognized. Bouchard (1976: 588) recognized no subspecies of *C. bartonii*, reporting that no characters separate the currently recognized subspecies. He also noted the instability of the rostral characters. Thoma (1982), Thoma & Jezerinac (1982), Jezerinac (1983), and Jezerinac et al. (1995) continued to use subspecific status for *C. carinirostris*.

We agree with Faxon (1914), Ortmann (1931), and Bouchard (1976) that the carina of *C. carinirostris* is an elusive trait, frequently absent or greatly reduced. In our study of the species we found the population in the vicinity of the type locality exhibited the carina most strongly and frequently, and in this respect one could conclude that *C. carinirostris* is a local varia-

tion. When we examined the *bartonii* complex for other traits, we noted clear differences in chela structure between populations of the Atlantic and Mississippi drainages in Pennsylvania (especially in form I males). Thoma & Jezerinac (1982: 137) reported that *C. carinirostris* could be distinguished from *C. bartonii bartonii* (Fabricius, 1798) by the thickened and frequently concave rostral margins; an abruptly ending rostrum that forms a 90° angle with the base of the acumen; more strongly developed postorbital ridges; stronger development of the lateral impression and dorsal ridges of the chela; a slight development of a second row of 2 or 3 tubercles on the mesial margin of the palm; reduced gape between the dactyl and propodus; and an enlarged third tubercle on the mesial margin of the opposable propodus. Continued work throughout the ranges of the two forms (and the rest of the range of the subgenus) revealed that the combination of thickened rostral margins, an enlarged third (or fourth) tubercle on the mesial margin of the opposable finger of the propodus, moderate development of the lateral impression and dorsal ridges of the chela, and less than 2 full rows of palmar tubercles is sufficient to distinguish this species from the nominate species and all other taxa presently known in the *bartonii* complex. The partial second row of palmar tubercles (not consistently present), 90° angled rostral margins, strong postorbital ridges, and dactyl gape are useful in distinguishing this species individually from other species of the *bartonii* complex. Within the subgenus two forms (*C. b. cavatus* Hay, 1902, and *C. sciotensis* Rhoades, 1944) consistently display the development of a second row of tubercles on the mesial margin of the palm. *Cambarus sciotensis* displays a full complement of 5 or 6 tubercles in the second row. Thoma & Jezerinac (1982) reported that *C. b. cavatus* consistently had 3 to 5 tubercles in the second row of palmar tubercles, noninflated rostral margins, and a narrower areola (the narrower areola may

relate to the burrowing habits of *C. b. cavatus*).

Principal component analysis of morphometric data for *C. carinirostris* and *C. b. bartonii* (Fig. 1) illustrates slight differences in body structure. The gape of the chela fingers, dactyl width, and areola width are the strongest loading variables (Table 1). Areola and dactyl width tend to be wider and chela gape narrower (Fig. 2) in *C. carinirostris*. No single body proportions are sufficient to separate the two taxa on a consistent basis. The most reliable character traits (using Form I males only) for consistently separating the two taxa are development of an enlarged third tubercle on the inner margin of the opposable propodus, lateral impression of the chela, and dorsal ridges on the chela fingers of *C. carinirostris* (Fig. 2). The northern form of *C. b. bartonii* (Atlantic drainage from the Potomac basin northward) lacks these chela characters altogether while the southern complex of *C. b. bartonii* lacks the lateral impression and thickened rostral margins. Some southern representatives of *C. b. bartonii* have an enlarged third tubercle on the opposable dactyl. This is accompanied by an enlarged first and fourth (occasionally third) tubercle on the opposable finger of the propodus, a characteristic lacking in *C. carinirostris*.

No intergrade populations have been found (using the characters we employed) between *C. carinirostris* and any other closely related taxon. For these reasons we elevate *C. carinirostris* to full species status. Important to note is that the above characteristics are most reliable in Form I males, preferably of a large size.

*Evolution, zoogeography and associated variation.*—*Cambarus carinirostris* is primarily an inhabitant of the still extant portions of the preglacial Pittsburgh River (Leverett 1902, Tight 1903) and (in part) the New River basin. This distribution is a reflection of the evolutionary history of the species. *Cambarus carinirostris* was most likely derived from an ancestral stock of the

*bartonii* complex that inhabited the New River (Kanawha basin). This stock was intern derived from populations inhabiting the upper Tennessee River basin, in particular the Clinch and Powell systems. Hobbs (1969) concluded that the subgenus *Cambarus* originated in the Tennessee basin and entered the Kanawha River basin from a northward migrating member of the “*extraneus* group.” We originally believed the subgenus *Cambarus* originated in the Kanawha basin (Jezerinac et al. 1995), but the recent discovery of a previously unknown archetypal *Cambarus* species (a description of this species and a discussion of its evolutionary significance is in development) in an isolated portion of what was once the Tennessee basin and now part of the Catawba River basin, confirms Hobbs’ conclusion.

Upon entering the New River basin through interdigitating headwater streams, probably in the Burk’s Garden area of Virginia, the ancestral *C. carinirostris* spread steadily through the system. *Cambarus carinirostris* probably was the first *Cambarus* to enter the upper New River system, thus having uninhibited dispersal opportunities. Access was gained to the preglacial Pittsburgh River basin in the headwaters of the Greenbrier River, again before other members of the subgenus *Cambarus*. No further dispersal occurred until postglacial times when *C. carinirostris* followed the retreating glaciers into the new Laurentian basin, where it established populations from the Genesee River of New York in the east to the Grand River of Ohio in the west. Dispersal on the western edge of the range was thwarted by the presence of crayfish populations (presently assigned to *C. b. cavatus*) that occupied the preglacial Teays River system (Jezerinac 1983). *Cambarus b. cavatus* most likely entered the Teays basin via the Big Sandy River. The Teays River population was a stream dwelling species of the subgenus *Cambarus* that apparently had ecological preferences similar to *C. carinirostris*. In the Allegheny Plateau portion of

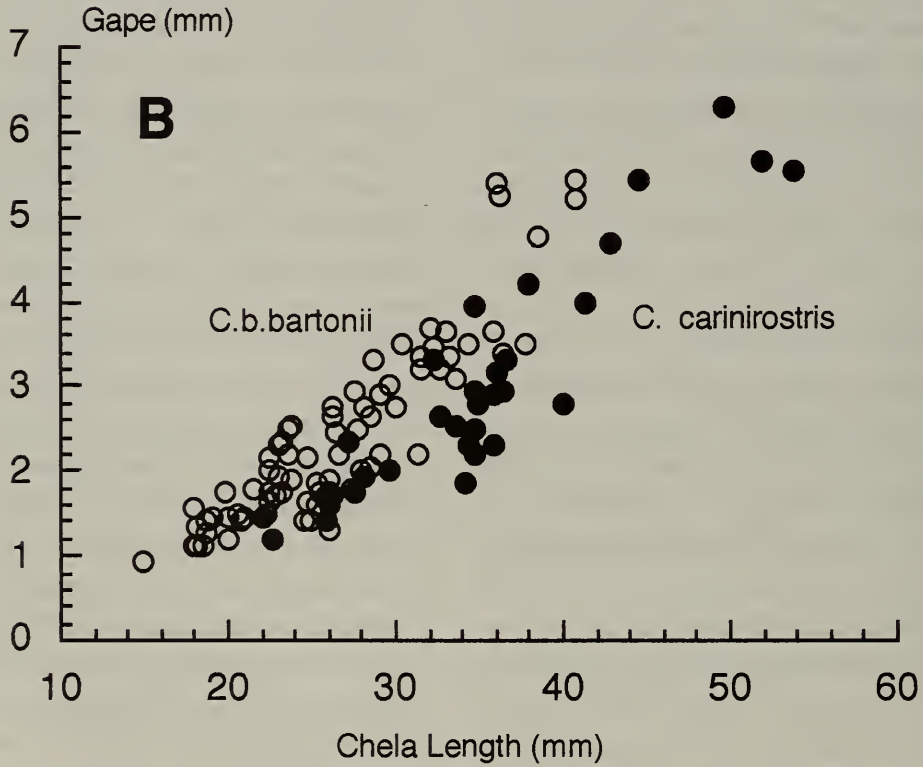
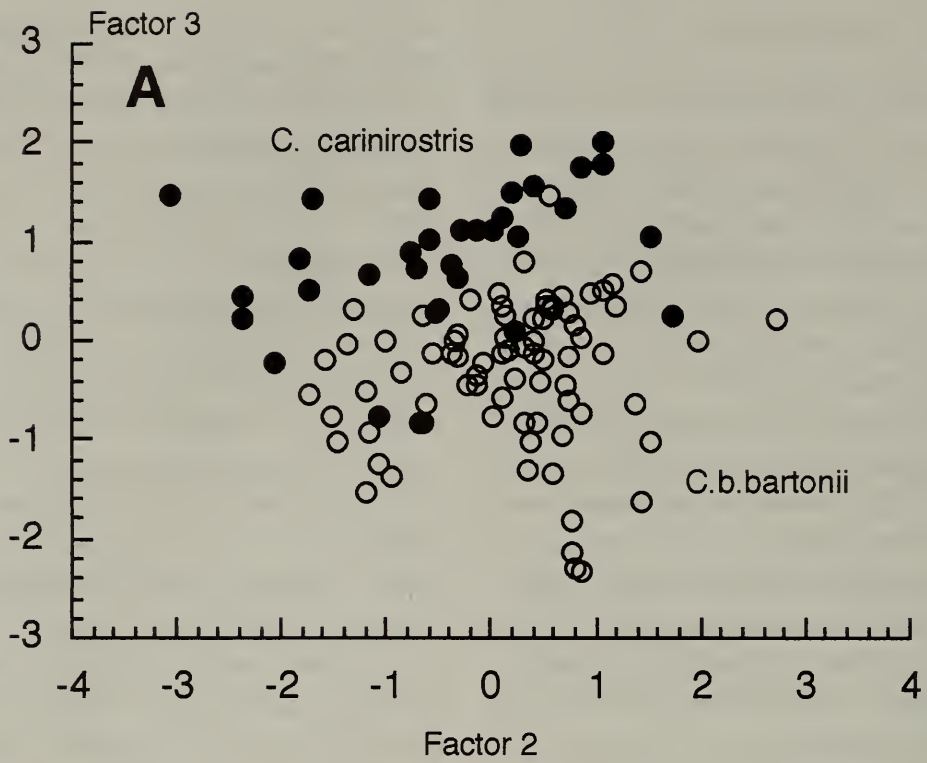


Fig. 1. A, Principal Component Analysis of *Cambarus carinirostris* (black circles, N = 33) and *C. bartonii bartonii* (open circles, N = 79) using Factors 2 and 3 (Table 1), Form I males only; B, Gape of chela fingers by length of chela for *C. carinirostris* (black circles, N = 33) and *C. b. bartonii* (open circles, N = 79), Form I males only.

Table 1.—Factor loadings for Principal Component Analysis of morphometric data of Form I male specimens of *C. b. bartonii* and *C. carinirostris*.

Measurement	Factor 2	Factor 3
Chela length	0.066	-0.044
Chela width	0.017	0.032
Chela depth	0.030	0.037
Gape of fingers	0.227	-0.326
Palm length	0.039	-0.031
Dactyl length	0.088	-0.042
Dactyl width	-0.095	0.394
Propodus finger length	0.045	-0.078
Propodus finger width	-0.076	0.120
Carapace length*	0.040	0.027
Carapace width	0.016	0.035
Areola length	0.110	0.023
Areola width	-0.667	-0.189

\* Measurement includes rostrum.

the New-Kanawha River basin and those streams draining to the Ohio River downstream of the Sardis Col, *C. b. cavatus* prevailed. In the newly formed Ohio River, the two species are presently found on their re-

spective preglacial sides of the Sardis Col, with neither having been able to advance into the other's range. To the north and to some degree to the east, the dispersal of *C. carinirostris* was inhibited by the presence of *C. b. bartonii*. It appears that the postglacial dispersal of *C. b. bartonii* (in the Atlantic slope drainage) was much more rapid than that of *C. carinirostris*, with *C. b. bartonii* effectively excluding *C. carinirostris* in those areas. Few opportunities existed for eastward dispersal of *C. carinirostris* in the Greenbrier, Monongahela, and Allegheny river basins because of physical barriers. Where potential stream piracies have been identified, no *C. carinirostris* could be found in Atlantic drainage streams. The ecological preferences of *C. carinirostris* and *C. b. bartonii* appear to be very similar.

*Taxonomic distinction.*—No other species in the subgenus *Cambarus* possesses the character combination of thickened ros-

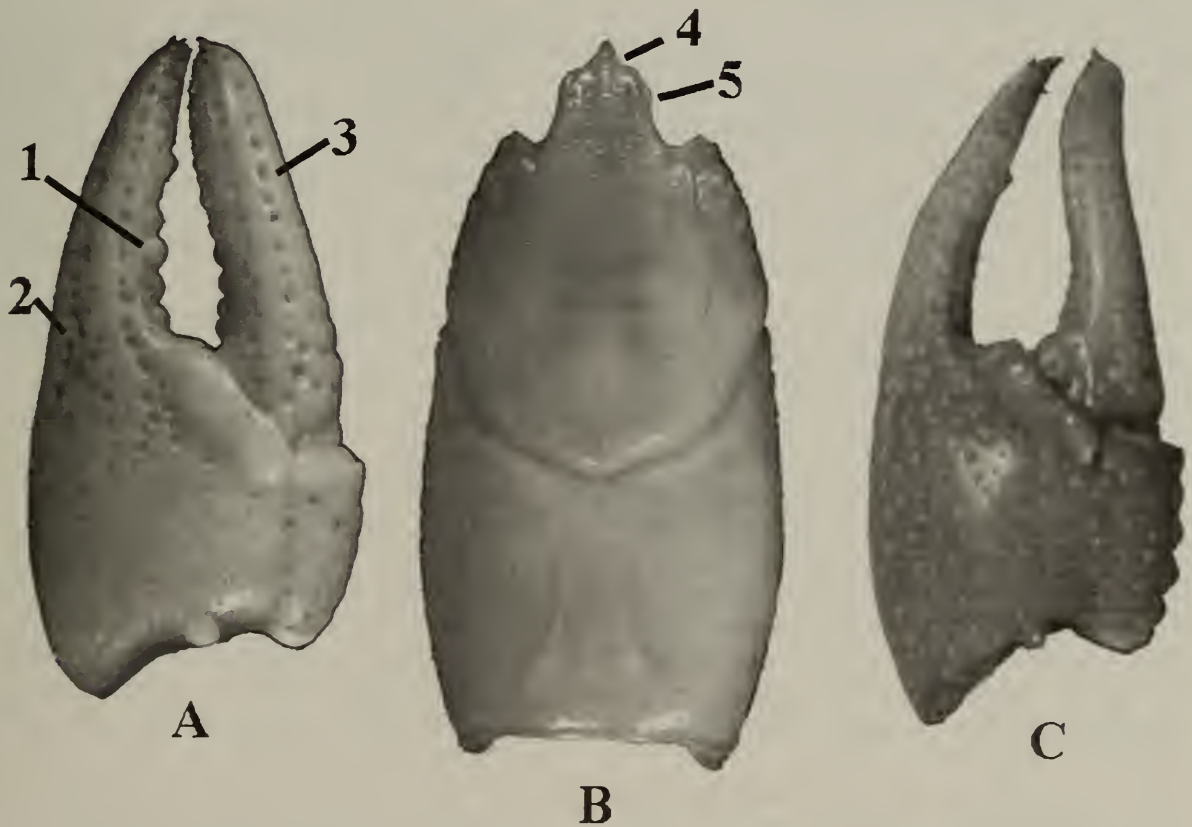


Fig. 2. A, Dorsal view of pereopod I chela of *Cambarus carinirostris*: 1—enlarged third tubercle on mesial margin of immovable finger, 2—lateral impression, 3—dorsal ridge; B, Dorsal view of carapace of *Cambarus carinirostris*; 4—rostral carina, 5—thickened rostral margins; C, Dorsal view of pereopod I chela of *Cambarus b. bartonii*.

tral margins, an enlarged third tubercle on the mesial margin of the opposable finger of the propodus, no enlarged tubercles on the mesial margin of the dactyl, moderate development of the lateral impression and dorsal ridges of the chela, and 1 row of palmar tubercles.

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